

COMPARATIVE STUDIES ON THE PERIPHERAL AND CENTRAL RETINA

V. THE SENSATION-TIME CURVE AND THE TIME COURSE OF THE FUSION FREQUENCY OF INTERMITTENT STIMULATION

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If two beams of light, the one intermittent at a rate above the fusion point, the other continuous, are led to the two halves of a photometric field and matched, this match should hold for all exposures of the beams down to about 4σ . The experiment is due to Piéron (1928) and implies that the Talbot-Plateau law is valid during the whole course of development of the sensation. Accordingly the time course of sensation of a fused intermittent light should follow curves of the type obtained by Broca and Sulzer (1902) in their classical work on the sensation-time curve. These authors matched a flash of variable duration with a steady light and from their results plotted curves showing the development of the brightness as a function of time of exposure. Previous and later contributions to the subject are summarized in a monograph by Bills (1920). The essential point, as far as our work is concerned, is that the brightness sensation rapidly develops to a maximum which lies between $40-150\sigma$ with intensities ranging from about $30-170$ lux. The stronger the stimulus, the higher the maximum, the shorter the plateau at this level, and the faster the drop to a lower level of brightness from which a more gradual fall, the local adaptation proper, sets in.

The fusion frequency, if a true index of brightness of sensation as borne out by numerous investigations, must necessarily reproduce this time course of sensation. On the other hand, there is evidence, to be pointed out later, showing that in most cases the critical frequency as an index refers to retinal processes alone, whereas the time course of sensation as determined by the method of Broca and Sulzer may involve a participation of higher centres more essential there than in the judgment of flicker or fusion.

The information that is wanted obviously concerns 1, the fusion frequency as a function of time of exposure, and 2, necessitates a determination of this function together with the sensation-time curve for the same light under identical conditions.

METHOD. The essential features of the apparatus have been previously (Granit and Harper, 1930) described. Two symmetrical 90° sectors are rotated in a light beam from a concentrated filament Mazda lamp, run at a constant voltage from a high capacity storage battery. The additional feature is a rotating shutter driven by a Telechron motor timed to make one revolution in two seconds. A mercury switch connected to a

TABLE 1
C = central, P = peripheral vision

		EXPOSURE IN σ										
		983	874	819	683	601	437	355	246	191	164	137
Area stimulated 3° of diameter												
130	C	57.6	56.3		55.7	54.4	52.1		45.7		39.4	34.2
	P	62.1	61.4		60.4		56.9		47.8		38.5	29.8
13.0	C	47.9	47.7		47.0	46.2	45.5	44.7	41.7	37.4		32.6
	P	52.8	52.3		51.7	51.1	49.6	48.8	45.8	39.6		31.2
1.30	C	36.1		36.0	35.4	35.2	34.7	33.9	32.9		30.3	27.4
	P	38.9		38.5	37.6	37.2	35.7	35.4	33.8	32.6	30.7	27.1
0.13	C	27.6			27.5		26.8		25.4		23.4	20.9
	P	29.0			28.9		28.1		25.9		23.8	20.7
Area stimulated 1° of diameter												
130	C	46.3	45.5		44.9	44.1	42.4	40.3	38.4	35.6		31.6
	P	44.9	44.9		43.6	42.2	40.7	38.5	36.4	32.4		26.8
13.0	C	41.7	40.9		40.3	39.8	39.1	38.1	36.6	34.5		29.9
	P	41.6	41.4		39.8	39.5	37.8	36.8	34.8	31.3		24.8
1.30	C	31.6	31.7		30.5	30.7	29.6	28.9	26.7	25.0	23.2	20.3
	P	30.4	30.4		29.3	29.3	28.1	27.9	26.3	24.8	23.5	20.0
0.13	C	23.3			23.3		22.5		21.2		17.5	14.9
	P	23.2			23.4		22.2		21.0		16.7	13.6

press button enables the observer to operate the shutter for single exposures. The first half of the total period of rotation gives the motor ample time to attain full speed with a light disc attached to it, the second half being used for varying the exposure. The experiments were performed binocularly in moderate light adaptation (see the previous paper) against a ground glass background which reflects about 0.007 millilambert. In

our opinion these are conditions which favour repeatability of the results over a long experimental period. A brighter background would be better still, but then low intensities could not be studied as easily.

The experiments then consist in determining the fusion frequency at different exposures of the flickering beam. At very short exposures the task is rather difficult and a great number of observations have to be taken for every single reading. This is especially the case at high intensities and the tendency there will be to underestimate the fusion point. The reason for that will later become apparent. For all intensities, however, it is true that two flashes and a dark interval are only visible as flicker when the phases are most favourably located with regard to the total time

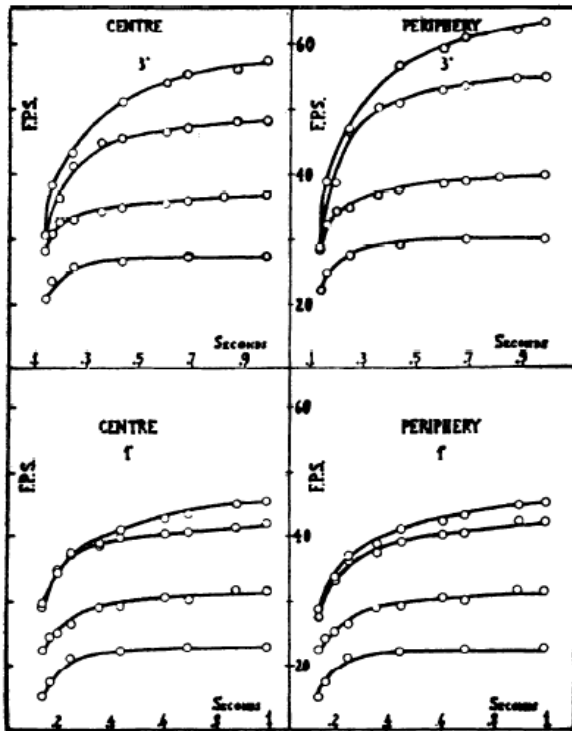


Fig. 1

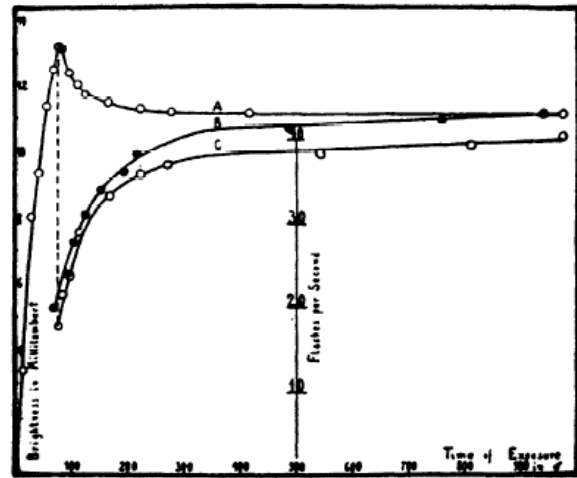


Fig. 2

of exposure. The criterion of fusion, accordingly, will have to be that in a *great number of trials* the flash must always look single. Some practice gives the required skill.

RESULTS. Typical results are shown in figure 1, and table 1 summarizes about 1100 individual determinations averaged from the data of the two observers. In the figure the diameter of the circles indicates the mean variation except in the case of the shortest exposures at high intensities where the mean variation is greater. The curves represent data obtained in a series of experiments on one observer and are for a 3° and 1° area in the center and with peripheral fixation at 10°.

The general result is clear cut. The fusion frequency increases with

time of exposure. The higher the intensity the longer the time necessary for reaching the maximal critical frequency even though the rate of rise is faster than at low intensities. There is also as stated above a relatively greater drop in the high intensity curves at short exposures. Increase of area stimulated affects the curve as does an increase of intensity and the moving of a *large* area towards the periphery. As previously pointed out and explained in this series (Granit and Harper, 1930) the difference between centre and periphery is a function of area and intensity of the stimulus.

With regard to our main problem it is evident that not only do these curves rise at a time when the ordinary sensation-time curves (Broca and Sulzer) fall, but, furthermore, the maximal fusion frequency is reached later at high than at low intensities. This also is precisely a reversal of the findings with the equality of brightness method and continuous light as used by Broca and Sulzer.

Comparison of flicker and sensation-time curves. In view of the results obtained in the experiments just described an apparatus was designed to make possible a determination of the sensation-time curves as well as of the time course of the critical frequency. Since this apparatus is a convenient unit for a number of different experiments on flicker and retinal interaction, all of which can be easily repeated and demonstrated, it is being described in a subsequent paper. At present it is sufficient to say that the light beam was split in two by means of prisms, with Telechron motors introduced into the one beam together with their respective shutters and timed to give different speeds in order to obtain the total range of exposures wanted.

By utilizing lenses the shutters were made to cut the beam at the focal point where its cross-section was only a few millimeters. The other beam was exposed throughout an experiment as comparison field and its intensity was adjusted by means of a carefully calibrated wedge covering a range of 1:2. A small balance wedge ensured homogeneity of the utilized section of the beam. Coarse adjustment was obtained with filters. A flashed opal glass was substituted for the ground glass on account of the fact that judgment as to brightness-differences is facilitated the more the surface approaches that of a perfect diffuser. Either or both beams could be flickered by introducing the rotating sectors at the desired point in the system.

To the observers the lights appeared as two adjacent semicircles together subtending 2° of diameter and seen against a fairly bright background of 0.195 millilambert. The experiment consisted in making a brightness match between the steady half and the flash at various times of exposure of the latter. This having been done the flash was made to flicker and its fusion point determined for various exposures. Central fixation and monocular vision were used throughout these experiments. Conditions in general were chosen so as to make for greatest possible accuracy. The

flickering semicircle was matched approximately with the steady half at each exposure so as to make the conditions with regard to interaction as comparable as possible in the two sets of experiments. It was found furthermore to be a great advantage to have a steady comparison field by which to judge as to flicker or fusion at short exposures. It was now possible to determine with a fair degree of accuracy the shortest exposure for flicker to appear.

The sensation time curve as averaged from 120 readings with two observers is plotted as *A* in figure 2. The brightness at the steady level¹ is 11.1 ml. This light was then flickered and the fusion point determined as a function of the time of exposure. Curve *C* gives the result. *A* shows how

TABLE 2

EXPOSURE	RISE OF BRIGHTNESS	EXPOSURE	INTERMITTENT LIGHT AT 11.1 ML.	EXPOSURE	INTERMITTENT LIGHT AT 22.2 ML.
σ	millilamberts	σ	flashes per second	σ	flashes per second
976	11.1	976	40.3	920	43.0
417	11.1	813	39.6	760	42.3
278	11.2	542	38.4	487	41.3
222	11.3	271	37.0	217	38.2
167	11.5	222	36.0	194	36.3
125	11.7	167	33.4	153	34.1
111	12.0	111	29.0	125	31.1
97.3	12.4	97.3	23.7	104	27.7
83.4	13.2	83.4	21.3	90.4	23.9
76.5	13.2	76.5	17.7	69.4	19.9
69.4	12.5				
55.6	11.4				
41.7	9.4				
27.8	8.0				
13.9	3.4				
0	Background at 0.195				

the first flash of *C* would rise if not restricted by the criterion of fusion. But *C*, of course, would always appear darker than *A*, since, on the Talbot Plateau law, the two 90° sectors reduce its brightness by 50 per cent. Hence, in order to obtain the flicker-time curve of a light which is of equal brightness with *A*, a light of 22.2 ml. was flickered. The result is given by curve *B*. The two flicker curves are averages of 160 observations. The data of figure 2 are tabulated in table 2.

¹ Bills (1920) prefers to plot the rise of the sensation in terms of just perceptible differences. The authors see no particular advantage in replacing brightness as measured photometrically by a still less interpretable unit. Bills also objects to the concept of the "steady level." However, both this method and the flicker method (Granit and v. Ammon, 1930) show that in *central vision* there is no drop in brightness between 1-3 seconds.

The curves show, as did the matching of the steady patch with the flickered half at the fusion point, that the two functions are altogether different. If A and C were equalized with the comparison field at about 1 second then it was necessary in both cases to raise the brightness in the comparison field at short exposures, just as shown by curve A , and this in spite of the fact that the fusion frequency as given by curve B or C was rapidly decreasing through that same interval. The brightness of the fused sensation obtained with intermittent light thus followed, at least in a general way, the sensation-time curve of the continuous stimulus. In other words, the time course of brightness in curve B follows approximately the course of brightness sensation shown in curve A . In order to find out precisely how A was matched by B , Pieron's experiment was repeated but with the flickered patch kept just at the fusion point. It was first matched with the steady comparison field at infinite exposure and the exposure then cut down for both simultaneously. At each stage the two were compared. Within the limits of error they were found to be approximately equal, except at the short exposures corresponding to the lower branch of the flicker curve where the fused intermittent light looked decidedly brighter. But as soon as the sectors were rotated at very high speeds, far above the fusion point, the brightness match established at long exposures again was fairly satisfactory at short exposures also.

The significance of this observation will become clear when the actual time relations are set forth. Let us consider the lowest point on B which is at a total exposure of 69.4σ and corresponds to a fusion frequency of 19.9 flashes per second with 50.3σ for each flash as well as for each dark interval. Even the most unfavourable sequence of phases, 9.5σ light, 50.3σ dark, and 9.5σ light, totaling 69.4σ , is perceived as a fused sensation, brighter than the one given by a 50 per cent less intense light, A , exposed continuously for 69.4σ . The total exposure of the flickered light can vary between 19.0 and 50.3σ with variation in the relative phases. If the quantity of light rather than the intensity were decisive these figures should be multiplied by 2 because A is at 50 per cent of the intensity of B and the range of variation would then be from 38.0 to 100.6 units. In this case only a certain percentage of the observations could give a greater brightness for the flickered patch, the steady patch being constantly illuminated for 69.4σ corresponding to 69.4 units in terms of quantities ($i \times t$). Obviously then it is not sufficient to multiply by 2 and the total quantity of light therefore does not determine the brightness at short exposures, but rather the rate at which this quantity enters the eye.

This conclusion is well substantiated by evaluating the curves published by Broca and Sulzer. They obtained sensation-time curves over a range of intensities and plotted them as above. Now, if the product of intensity and time of exposure were a constant ($it = c$), then a line parallel with the

abscissa and cutting a family of sensation-time curves obtained at different intensities of stimulation gives a constant level of brightness which is the index wanted for the product $i \times t$. In this way it is possible to determine whether a constant level of brightness corresponds to a constant amount of energy or whether the rate of the processes concerned is also significant. If the ordinate used as index be about 12 lux it will be found by graphical examination of Broca and Sulzer's curves that for the intensities 170,126 and 64.5 lux the products $i \times t$ relate roughly as 17:29:82 for the constant level of brightness. Mere inspection of their curves shows that the relation is of this type. The higher the intensity of stimulation, the greater the rate at which the processes underlying brightness develop.

Such a relation is evidently to be expected from work on other sense organs. Direct evidence has been obtained by Adrian (1928) and by Matthews (1931) by recording nerve impulses from muscle spindles and pressure end organs. On the sensory side there are also the results obtained by v. Frey on touch (1929). Furthermore, as is well known, the rate of stimulation determines the efficacy of a muscle or nerve stimulus.

We may safely conclude that at short exposures the rate of stimulation is relatively more important than the total amount of energy and that the sensation-time curve expresses this fact. How precisely, we do not know, since it is not clear whether at each exposure the brightness match refers to the final level of brightness reached at the end of that exposure or is some complex integrated function of all the stages the process has traversed during the total time of exposure. At long exposures the rate of stimulation, of course, loses in significance.

Whereas the general nature of the sensation-time curve is indicated in a fairly direct way by the experimental evidence it is more difficult to know what lies behind the fusion frequency-time curves. The time relations of the "peak" of the sensation-time curve show that the fusion frequency is not determined by the fusion of such peaks since the frequency at this point would be only about 11 f.p.s., whereas the corresponding critical frequency actually is about 23 f.p.s. for curve *C*. On the other hand the rate of rise of the sensation certainly is reflected in the fusion frequency. Thus Ives (1922) found that when rotating sectors were cut so as to give the same mean brightness but brought the light on more or less gradually, the one which produced the most rapid development of illumination gave the highest critical frequency. The effect, however, also depended upon the amplitude of the wave, the rate of onset being relatively more important at small amplitudes. In the retinal action potential Piper (1911) found the "peaks" in flicker to correspond to the rapidly rising b-waves in the well known onset of potential change. The criterion of fusion implies, as shown by our results, that the rising phase of the sensation-time curve is cut off before the maximum has been reached. The only direct correla-

tion between the peak in *A* and curve *C* is that the shortest time within which flicker can be perceived is identical with the time necessary for the sensation to reach its maximal point (cf. the vertical line in fig. 2). The peak, of course, will seriously interfere with the perception of flicker at high intensities and short exposures. Thus the flicker curves at high intensities will become relatively too low at short exposures (cf. fig. 1).

Two facts which on the surface appear to be contradictory will have to be kept in mind when discussing the nature of the fusion frequency as an index of brightness. The one is that an array of experimental evidence, part of which was mentioned in a previous paper in this series (Granit and Harper, 1930) indicates that the fusion frequency records the intensity of the physiological process underlying the perception of brightness. The other one is the very striking fact, illustrated by figure 2, that at certain exposures the fusion frequency and the brightness perceived alter in a different direction (cf. curves *A* and *C* in the region following the peak). The latter observation may be amplified by the following experiment: If at an exposure of about 1 second a brightness be chosen which gives a fusion frequency of about 20 f.p.s. it is found that, when this critical frequency is located on curve *B*, the sensation as given approximately by *A* corresponds to about 13 ml. The brightness which has to be used at the long exposure for giving the same response in terms of fusion frequencies is then only about 0.3 ml. How is it possible that the fusion frequency can be a criterion of brightness and at the same time not correlate in a given way with brightness? Undoubtedly equal fusion frequencies must imply that the processes responsible for fusion are equal. The individual peaks in the flickered lights must for a given fusion point rise from the same initial level to the same height and they must leave excitatory remainders of equal duration to account for the fact that equally long dark intervals are non-visible. The time course of such excitatory after-effects was plotted in the previous communication (Granit and Davis, 1931) for subliminal flashes.

The answer to all these questions can only be given by an assumption fairly well limited by the above considerations, namely, that the fusion frequency is an index showing the level of an excitatory state in the retina. There seems to be no way of relating fusion frequency to brightness unless it be assumed that this is the case. Owing to the fact that the sensation at short exposures is determined by the rate at which the excitatory state is formed, and to the participation of higher centres into which this "reaction to the rate" is propagated, the brightness at short exposures does not correlate with the level of excitatory state in the retina.

As a matter of fact all the evidence available shows that under simple conditions the fusion frequency is determined by retinal processes alone. Sachs (1929) states in a short communication (based on work which is

extensively reviewed by Kohlrausch, 1931) that in taking action potentials from his own eye, as previously done by Hartline (1925), flicker as perceived corresponded to small waves superimposed upon the action potential whereas fused intermittent light gave the ordinary smooth wave. Kohlrausch concludes that the flicker method reproduces purely retinal conditions. Adrian and Matthews (1928) found that the fusion point defined as asynchronism of impulses arriving through the optic nerve of the eel's eye behaved, with regard to area and intensity, like the seen fusion point of the visual experiment. Piper (1911) has published extensive series of retinal action potentials obtained from various vertebrate eyes in response to intermittent stimulation. Here as in the work of Sachs flicker is found to be small waves superimposed upon the slow phase of the action potential and at certain rates of intermittency fusion appears. In addition there is the fact, noticeable, for instance, in his figures 20-22, 25, 27-29, 36, 37, that a constant rate of flicker does not burst through the action potential until several flashes have passed. This, of course, is precisely what on the basis of our experiments should be expected.

It would seem, therefore, as if our experiments should be repeated on excised eyes before the theoretical analysis is carried further. If then new correlations could be established our results might serve as a basis for quantitative treatment. Purely empirical equations, in our opinion, deserve little attention. As to the general question whether the process is localized in the retinal neurones or in the receptors, the former assumption seems more probable, since it is easy to show by taking two areas some distance apart that the synaptic lateral components influence these flicker curves considerably (cf. also previous communications by Granit, 1930; Granit and Harper, 1930; and the following paper in this series, Graham and Granit, 1931).

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SUMMARY

The development of the fusion frequency as a function of time of exposure has been studied in central and peripheral vision with a 1° and a 3° area.

The fusion frequency increases first rapidly, then slowly with time of exposure. The higher the intensity, the steeper the rise and the longer the time to the maximum.

Increase in area affects the time course of the fusion frequency as does an increase in intensity and as does the moving of a large area towards the periphery (at 10°).

The curve showing the development of the sensation of brightness has

been obtained under conditions identical with those used in measuring the time course of the critical frequency. In plotting the two sets of data to the same abscissae (time of exposure) and correlating them it becomes evident that the two functions are different, in spite of the fact that the flicker phenomenon is an index of brightness. The nature of this discrepancy is analyzed.

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